

# Scale and landscape perception: the case of refuge use by Boreal Toads (*Anaxyrus boreas boreas*)

Z.L. Long and E.E. Prepas

**Abstract:** Refugia likely represent a critical resource necessary for the persistence of populations of Boreal Toads (*Anaxyrus boreas boreas* (Baird and Girard, 1852)) in a given area. However, the features that define suitable refuge microsites and the extent to which the habitat surrounding refugia is exploited remains unclear. We sought to describe refuge characteristics in the context of their surroundings and to determine whether local-scale movement behaviour associated with refuge use might provide a novel perspective of landscape-level habitat selection. A pilot study suggested that refugia were selected primarily for physical structure in the form of coarse woody debris, but this was not the case. Instead, refugia provided favourable microclimates with elevated relative humidity compared with the surrounding habitat. Boreal Toads tended to forage at night within 15 m from refugia. This distance was used to calculate activity centres across toad summer home ranges. Activity centres prioritized the importance of treeless habitat overall and wetland habitat for females when compared with 50% core home ranges. This approach could be used to pinpoint critical habitat at the landscape scale, which may be of particular importance for conserving populations currently in decline.

**Key words:** Boreal Toad, *Anaxyrus boreas boreas*, refuge microsites, local-scale movement, habitat selection.

**Résumé :** Les refuges représentent vraisemblablement une ressource essentielle nécessaire à la pérennité des populations de crapaud boréal (*Anaxyrus boreas boreas* (Baird et Girard, 1852)) dans une région donnée. Cependant, les caractéristiques qui définissent les microsites de refuge convenables et la mesure dans laquelle l'habitat entourant ces refuges est exploité demeurent méconnues. Nous avons tenté de décrire les caractéristiques des refuges dans le contexte de leurs environs et de déterminer si le comportement de déplacement à l'échelle locale associé à l'utilisation de refuges peut offrir une nouvelle perspective sur la sélection de l'habitat au niveau du paysage. Une étude pilote a suggéré que les refuges sont sélectionnés principalement pour leur structure physique, soit des débris ligneux grossiers, mais cela n'était pas le cas. Les refuges fournissaient plutôt des microclimats favorables caractérisés par une plus forte humidité relative que l'habitat environnant. Les crapauds boréaux tendaient à se nourrir la nuit dans un rayon de 15 m d'un refuge. Cette distance a été utilisée pour calculer les centres d'activité à l'échelle du domaine vital estival des crapauds. Les centres d'activité reposaient prioritairement sur l'importance des habitats sans arbre en général et des habitats de milieux humides pour les femelles en particulier. Cette approche pourrait être utilisée pour cerner les habitats essentiels à l'échelle du paysage, qui pourraient s'avérer particulièrement importants pour la conservation de populations actuellement en déclin.

**Mots-clés :** crapaud boréal, *Anaxyrus boreas boreas*, microsites de refuge, déplacement à l'échelle locale, sélection d'habitat.

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## Introduction

The use of refuge microsites (i.e., refugia) has been well documented in many amphibian species and individuals often display a high degree of fidelity towards them. This suggests that these microsites likely represent a critical resource necessary for survival. Refugia are often structurally diverse, with multiple refuge types being exploited within a population (Schwarzkopf and Alford 1996; Seebacher and Alford 1999; Bull 2006). These microsites are particularly important to poikilotherms because, in addition to shelter, they provide favor-

able microclimates necessary for thermo- and hydro-regulation (Duellman and Trueb 1994). Moisture may be more important than temperature for amphibians (e.g., Bartelt et al. 2004), because their physiology makes them particularly susceptible to desiccation. However, what constitutes suitable refugia is unclear (Shoo et al. 2011) and likely to vary among species.

Radiotelemetry studies have documented that refugia are generally occupied during the day (Cohen and Alford 1996; Bull 2006), with the assumption that the occupants leave to forage the surrounding habitat at night when predator, temperature,

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and desiccation stresses are low (Forester et al. 2006). In this respect, these species behave as central-patch foragers, likely exploiting several patches over the course of the summer. Intrinsic to this behaviour are homing abilities used to orient towards breeding sites, foraging grounds, and shelter (displayed by many amphibians; e.g., Sinsch 1987; Rittenhouse and Semlitsch 2009), which imply that individuals possess some measure of spatial memory. Information collected at the local scale is theoretically comprehensive because animals are able to sample an entire area (Orians and Wittenberger 1991; Indermaur et al. 2009), with knowledge decreasing outward from the centre, or refuge in this case (Fauchald 1999; Roshier et al. 2008). It is likely that foraging takes place within this familiar space and that maximum foraging distances from refugia represent "activity centre" patch boundaries.

Activity centres represent the habitat most frequently exploited and likely to be critical to the persistence of a species. Forester et al. (2006) suggested that home ranges of the American Toad (*Anaxyrus americanus* (Holbrook, 1836)) might be better represented by a series of activity centres and narrow movement corridors connecting them, based on their overall movement behaviour. This approach has merit, but their activity centre boundaries were arbitrarily selected and not based upon local-scale movement behaviour. Although these areas would still be captured by more conventional home-range estimations, the relative proportion of the different habitat types would most probably vary between techniques. If individuals were preferentially selecting scarce habitat types for their activity centres, these habitats might be overlooked within larger home-range estimates.

The goals of our study were to describe habitat selection and local-scale movement behaviour associated with refuge use by Boreal Toads (*Anaxyrus boreas boreas* (Baird and Girard, 1852)) and to assess how our perception of landscape-level habitat use might change by incorporating local-scale movement information. The Western Toad (*Anaxyrus boreas* (Baird and Girard, 1852)) is a species of conservation interest in North America owing to several documented declines throughout its global range (Hammerman et al. 2004). However, populations of Boreal Toads in Canada appear to be stable or expanding, particularly in the Boreal forest (Wind and Dupuis 2002). Refugia likely represent a critical resource necessary for the persistence of populations of Boreal Toads. However, the features that distinguish refugia from their surroundings are unclear, as is the degree to which the area surrounding refugia is exploited (Smith et al. 2003).

Our study tested whether Boreal Toad refugia were selected for physical structure, specific ground-layer vegetation or microclimate, and whether refugia were distinct from their surroundings. We conducted a pilot study in 2008, from which we predicted that refugia would be selected primarily for physical structure in the form of coarse woody debris (CWD); we expected CWD abundance and volume to decline with distance from refugia. The pilot study further suggested that the toads were not selecting refugia for specific ground-layer communities. Refugia were also expected to provide favourable microclimates, with moisture likely being more important than temperature. In addition to refuge features, we investigated how local-scale movement behaviour associ-

ated with refugia might be used to provide a novel perspective of landscape-level habitat selection. We expected that activity centres would prioritize different habitats when compared with more conventional home-range estimations.

## Materials and methods

### Study area

Four wetlands were selected within 50 km of Whitecourt, Alberta (54°8'34.1"N, 115°41'6.9"W; NAD 83). Each wetland was within a spatially discrete forest stand, two dominated by lodgepole pine (*Pinus contorta* var. *latifolia* Engelm. ex S. Watson) and two dominated by balsam poplar (*Populus balsamifera* L.) and trembling aspen (*Populus tremuloides* Michx.). White spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) also occur throughout the region. The study area falls within the western Boreal Plain ecozone of Canada, where mean daily temperatures range from -17.5 to -22.5 °C in January and 12.5 to 17.5 °C in July (Parks Canada 2009). Mean annual precipitation (300–500 mm) is often equal to or exceeded by annual surface evaporation (300–700 mm; Fisheries and Environment Canada 1978), making this landscape relatively dry.

### Patterns of refuge use

Radiotelemetry data were collected from 35 toads (16 males and 19 females) from April through September 2009 and 2010. Individuals were located during the day, on average, once every 24–48 h for periods ranging from 2 to 126 days. This sampling interval was selected due to logistic constraints (number of animals and distance between sites). Radio transmitters (1.6 g BD-2; Holohil Systems Ltd., Carp, Ontario, Canada) were attached via external waistband harnesses fashioned from stretch bead cord (Baldwin et al. 2006). See Long et al. (2010) for a detailed description of this attachment technique. Transmitters weighed <5% animal body mass in all cases.

Radiotelemetry provides point data useful for determining seasonal movement patterns and is indispensable for finding occupied refugia. However, telemetry does not provide useful information on the local-scale movement behaviour within the described sampling interval. Fluorescent powder and UV-light night tracking was used to determine patterns of refuge use and local-scale movement behaviour for 7 refugia in 2009. Refugia were selected for night-tracking opportunistically and timing depended on weather conditions (i.e., several days without precipitation) and the individual behaviour of the animal (i.e., animals that had already occupied a refuge for a long period were less likely to abandon their refugia following pigment application). Orange fluorescent pigment powder was deposited at refuge openings or directly on animals when they were either partially or fully exposed. Powder on the animals transferred to vegetation and debris that they contacted during their nocturnal movements, which then luminesced under UV light. Distances travelled and corridor use was recorded for 1–3 nights following powder deposit. Fluorescent powder remained visible on the animal and environment after this period, but it became relatively inert and would not readily transfer.

Refuge characteristics

A refuge was defined as a microsite often no larger than the individual, providing shelter in most cases, and occupied for a period  $\geq 5$  days. Once refugia were identified, a series of ten 1 m<sup>2</sup> plots were established: 1 m<sup>2</sup> plots were sufficient to describe refugia in the context of their immediate surroundings. Plots were separated into three categories based on distance from refugia. A plot was established directly over the refuge (refuge), four plots were established immediately adjacent to the refuge plot and oriented to the cardinal directions (near-refuge; NR), and five additional plots were randomly distributed within a 20 m radius from the refuge centre (random; RAN). This radius was selected to reflect the local-scale movement behaviour described with night tracking.

A total of 26 refugia (260 plots) distributed among 20 animals were sampled (Table 1). These animals were collected either at breeding wetlands early in spring ( $n = 11$ ) or in the surrounding uplands as the summer progressed ( $n = 9$ ). GPS coordinates were collected at each refuge location, which were then used to determine the distance from breeding site (when known;  $D_B$ : m), and all surface-water features, including confirmed breeding sites, streams, and all other wetlands ( $D_W$ : m). Several data sets were collected from the plots.

Community data

Percent cover of vegetation by species and growth form (i.e., groups that would likely serve the same function for toads) were measured. The nine vegetation growth forms were (1) mosses, club mosses and liverworts; (2) ferns and horsetails; (3) graminoids; (4) short forbs (<40 cm); (5) tall forbs ( $\geq 40$  cm); (6) creeping shrubs; (7) short shrubs (<1 m); (8) tall shrubs ( $\geq 1$  m); and (9) mushrooms and lichens.

Environmental data

Percent cover of exposed soil, water, stone, litter (including dead grass) and CWD, and crown closure (%), as well as CWD volume (CWDv: m<sup>3</sup>/ha), were measured. Crown closure was estimated using a convex spherical densitometer; four measurements (oriented to the cardinal directions) were taken at each plot and averaged together. Canopy measurements with densitometers are often biased (Nuttle 1997); however, fine differences in canopy cover were not explicitly important in our study (as in Bartelt et al. 2004). CWDv was estimated from length and width measurements taken from all CWD with a diameter  $\geq 5$  cm.

Soil data

Temperature ( $^{\circ}$ C), moisture (% volume), and compaction (kg/cm<sup>2</sup>) were measured. Soil characteristics were averaged from three randomly selected points in each plot. Temperature and moisture were measured with a Delta-T WET Sensor (at a depth of  $\sim 10$  cm). Soil compaction was measured with a pocket penetrometer (Forest Suppliers Inc.).

Microclimate data

Temperature ( $T$ :  $^{\circ}$ C) and relative humidity (RH: %) were collected from a total of 10 refugia (4 refugia in 2009 and 6 refugia in 2010). As with night tracking, refugia were selected opportunistically. Microclimate data were restricted by

Table 1. Summary of refuge structure and use by individual male and female Boreal Toads (*Anaxyrus boreas boreas*).

Unique refuge	Animal	Year	Microhabitat	Strategy	Residence (days)
Males (M)					
1	M1	2009	CWD	C3	10
2		2009	EXP	C4	37
3		2009	BRW	B1	19
4	M3	2009	EXP	C4	19
5	M4	2009	BRW	B2	10
13	M5	2010	CWD	C1	7
14		2010	VEG		50
15	M6	2010	BRW	B1	10
16		2010	EXP		27
17	M7	2010	CWD	C1	12
18	M8	2010	VEG		25
19	M9	2010	VEG		18
Females (F)					
6	F1	2009	CWD	C3	13
7	F2	2009	CWD	C1	38
8		2009	CWD	C2	7
9		2009	EXP	C4	46
10	F4	2009	BRW	B1	14
11		2009	BRW	B2	28
12		2009	CWD	C2	10
20	F6	2010	VEG		46
21	F7	2010	VEG		41
22		2010	BRW	B2	11
23		2010	CWD	C1	27
24	F9	2010	CWD	C1	7
17		2010	CWD	C3	33
25		2010	EXP		22
26	F11	2010	CWD	C2	10
19		2010	VEG		16

**Note:** Microhabitat abbreviations are as follows—CWD: coarse woody debris; BRW: burrow; VEG: vegetation; EXP: exposed. Refugia using coarse woody debris or burrows were split into substrategies—C1: cavity within CWD; C2: sheltered by CWD with no physical contact; C3: CWD and ground interface; C4: exposed, but resting atop CWD; B1: shallow burrow in substrate; B2: deep burrow in soil.

cost (the number of weather stations/data loggers available) and animal behaviour (data were only desired while refugia were occupied). Kestrel 4000 pocket weather stations were used in 2009; three weather stations (one in each plot category) were established per refuge. DS1923-F5 Hygrochron Temperature and Humidity iButtons were used in 2010; five iButtons (one in the refuge plot, two in NR plots, and two in RAN plots) were established per refuge.

Data analysis

Refugia were split into four refuge types based on dominant physical structure: CWD<sub>R</sub> (coarse woody debris), BRW (burrows, in litter or soil), VEG (vegetation), and EXP (exposed, no cover). Nonmetric multidimensional scaling (NMS: a form of ordination used for data visualization) was conducted to visualize and explore ground-layer community data. We used Sorensen's distance measure (because of the nonlinear nature of the data), and ran the ordination using the "slow and thorough" autopilot option in PC-ORD (McCune and Mefford 2005). NMS simply presents the

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strongest trend but does not summarize data like principle component analysis would, so we ran the test five times to ensure our results were consistent. We then ran a multi-response permutation procedure (MRPP: a nonmetric analogue of discriminant functions analysis) to test for potential plot category grouping effects on ground-layer community structure. Tests were run by both species and growth form.

Environmental, soil, and microclimate data (i.e., refuge characteristics) were analysed separately from vegetation communities. A simple microclimate index was constructed by taking the difference between a given refuge (assigned a value of 0) and corresponding NR and RAN plot T and RH values. Scaling the microclimate data relative to refugia helped control for temporal variation, as all refugia were not sampled concurrently because data collection depended entirely on each animal's unique behaviour.

Kruskal–Wallis analysis was used to investigate refuge characteristics (i.e., environmental, soil, and microclimate data) among plot categories. Nonparametric tests were appropriate because the data set was non-normal and could not be suitably transformed for normality or homogeneity of variance. Distance data (i.e.,  $D_B$  and  $D_W$ ) were square-root-transformed for normality and analysed by sex and time (month) with an analysis of variance (ANOVA). Refugia were considered discrete units, even in instances where multiple refugia were sampled from the same animal or when a refuge was shared by several animals. We acknowledge the issue of statistical independence in this analytical approach, but refugia were the sampling unit of interest in this study, not the individual.

Providing that the toads forage at night, the distance travelled to and from refugia likely represents the radius for areas with the most intensive resource exploitation. We calculated activity centre areas for all 35 toads using fixed kernel density home-range estimation that was adjusted to reflect the night-tracking distances. We also calculated 50% fixed kernel home-range estimates for each animal. Both home-range estimates were constructed using the Home Range Tools (HRT: Rodgers et al. 2007) extension for Arc-Map (ESRI® (Environmental Systems Research Institute) Inc., Redlands, California, USA). We then compared the proportions of different habitat types between the 15 m activity centre and 50% core home-range estimates using a  $G$  test. Habitat was defined by dominant vegetation at two scales: stand type (wetland, grass and shrub, deciduous, coniferous) and canopy (open and closed). Habitat categories were derived from the forest inventory; closed-canopy habitat consisted of all areas dominated by trees, while open-canopy habitat consisted of areas dominated by grasses, shrubs, and wetlands. Anthropogenic (cutblocks, roads, and seismic lines) and natural clearings were grouped together.  $G$  test compare the similarity of two distributions and is typically performed on count data. Our data set, however, was best expressed by averaging across multiple individuals, resulting in each habitat type being presented as a mean and associated standard error (SE).  $G$  tests do not accommodate this internal variation and operate entirely on the mean values. We acknowledge the limitations of this analysis, but we believe this technique is suitable for illustrating underlying trends in our data.

## Results

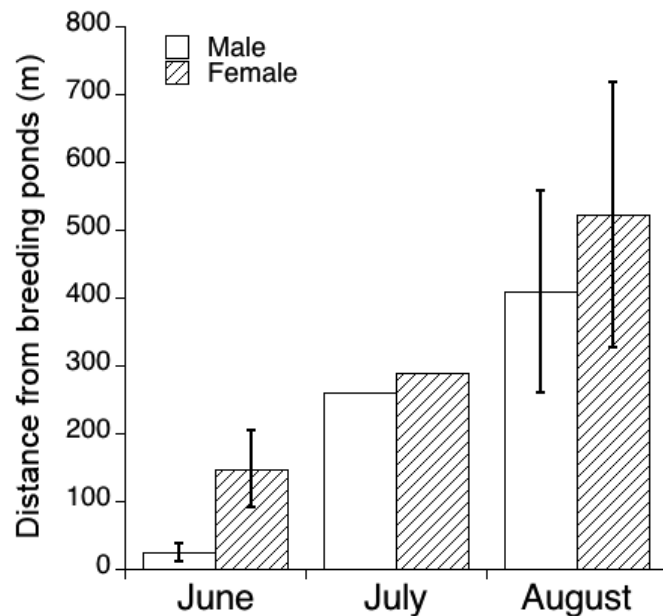
### Patterns of refuge use

Toads used, on average, 1.3 refugia over the course of this study (12 individuals each used a single refuge and 8 individuals used two refugia), which were occupied for  $22 \pm 3$  days (range 7–50 days; Table 1). We were unable to follow individuals throughout their postbreeding activity, so it is likely that toads exploited additional refugia over the summer. Refugia were established increasingly farther from breeding sites as the summer progressed ( $D_B$ :  $F_{[2,14]} = 5.63$ ,  $p = 0.02$ ); females tended to establish their refugia farther from breeding sites than males early in the summer, but males eventually caught up (Fig. 1). Males and females established their refugia at similar distances from all surface water features ( $D_W$ :  $125 \pm 51$  and  $131 \pm 35$  m, respectively; range 1–571 m).

The dominant refuge type was CWD<sub>R</sub> (10 refugia (38%; Table 1). If we include EXP refugia that were established on top of woody debris, 13 refugia (50%) used CWD in some form. Of the remaining refugia, 6 (23%) were BRW, 5 (19%) VEG, and 5 (19%) were EXP (or 2 (8%) excluding those located atop CWD). Six refugia were closely associated with basking sites and surface water; five of these refugia were VEG or EXP. The refugia occupied longest in 2010 (two females for 41 and 46 days, and a male for 50 days) were immediately adjacent (<0.5 m) to small pools of water or shallow (~2 cm) standing water, and three more were located at the edges of wetlands. Multiple refuge strategies were associated with animals using CWD<sub>R</sub> and BRW refuge types. Individuals that occupied multiple refugia did not appear to preferentially select microsites with similar characteristics (Table 1). In 2010, two refugia were each occupied by two toads (one male, one female) simultaneously: one refuge was in a CWD cavity, while the other was under shrubs (genus *Salix* L.) at the bottom of a depression with exposed soil at the edge of a beaver pond (water <1 m). In the same year, two female toads in succession occupied a refuge characterized by moss substrate under shrubs (*Salix* spp.) near surface water <0.5 m deep.

The mean straight-line distance travelled before returning to refugia in a single night was ~15 m (median 15 m, range 8–18 m). Most individuals travelled in linear paths, leaving and returning using the same routes over multiple nights. One male and two females travelled in straight lines between closely associated refugia. Most travel routes occurred on the surface in areas with short to no vegetation, but some individuals made use of tunnels (e.g., root systems, hollow logs, and squirrel middens) or travelled along the tops of downed logs. Some individuals made extensive use of the structure provided by CWD. For example, a female toad in the pilot study (not included in these analyses) used a cavity at the top of a stump ~1.5 m high and two females from 2009 used suspended logs. Our observations suggested that certain toads used landmarks to navigate. There were two female toads that left their refugia in straight lines, hooked around a tree before continuing, and hooked back around the same side of the tree when returning. A single female was observed engaging in circular search patterns in opposing directions, resulting in a figure-8 pattern over 2 nights; she ventured only 8 m from the refuge.

**Fig. 1.** Refuge distances (mean  $\pm$  SE) from breeding sites by month for 7 male and 10 female refugia of Boreal Toads (*Anaxyrus boreas boreas*).



### Refuge characteristics

Clearings up to 325 m and forest edges were not barriers to movement of Boreal Toads. Most (54%) refugia were established in clearings and were located  $19 \pm 5$  m from the nearest forest patch or edge. The remaining refugia were established in forested areas and were  $40 \pm 6$  m from edges. This strip of habitat along forest edges accounted for ~25% of the total landscape over which the toads ranged. NMS produced a three-dimensional model that accounted for 65% of the variation expressed in the ground-layer community by species, but no grouping among categories was identified by MRPP ( $p = 0.49$ ). The NMS model for growth forms was more robust, accounting for 79% of the variation. Again, however, MRPP did not identify grouping among categories within the data ( $p = 0.15$ ). Furthermore, environmental parameters did not differ among categories ( $p \geq 0.19$  in all cases). Although CWD volume and percent cover appeared to decrease with distance from refugia (i.e., rank order), this relationship was not significant ( $p = 0.32$  and  $0.19$ , respectively). Likewise, temperatures were similar among refuge, NR, and RAN areas ( $\chi^2_{[2]} = 1.40$ ,  $p = 0.50$ ). Relative humidity was greatest in refuge plots ( $\chi^2_{[2]} = 7.49$ ,  $p = 0.03$ ) and decreased with distance from refugia (Figs. 2a–2b).

### Home-range estimation

From night-tracking distances, we determined that 15 m represents a realistic patch radius whose area is accessible (and likely to be exploited) by an individual at any given time. Total activity centre areas were  $0.57 \pm 0.06$  ha for males and  $0.55 \pm 0.07$  ha for females. There were no differences in the habitat proportions between activity centre and core home-range areas at the stand-type level when pooling all individuals ( $G = 5.07$ ,  $p = 0.17$ ); however, open habitat was under-represented in the 50% core home ranges ( $G = 4.24$ ,  $p = 0.04$ ; Fig. 3a). Male habitat proportions were similar between estimation techniques (stand type:  $G = 4.44$ ,  $p =$

$0.22$ ; canopy:  $G = 1.08$ ,  $p = 0.30$ ). For females, wetlands made up a larger proportion of activity-centre habitat when compared with the 50% core home ranges ( $G = 19.92$ ,  $p < 0.01$ ), which was also reflected in the differences between open and closed habitat ( $G = 8.37$ ,  $p < 0.01$ ; Fig. 3b).

## Discussion

### Refuge characteristics

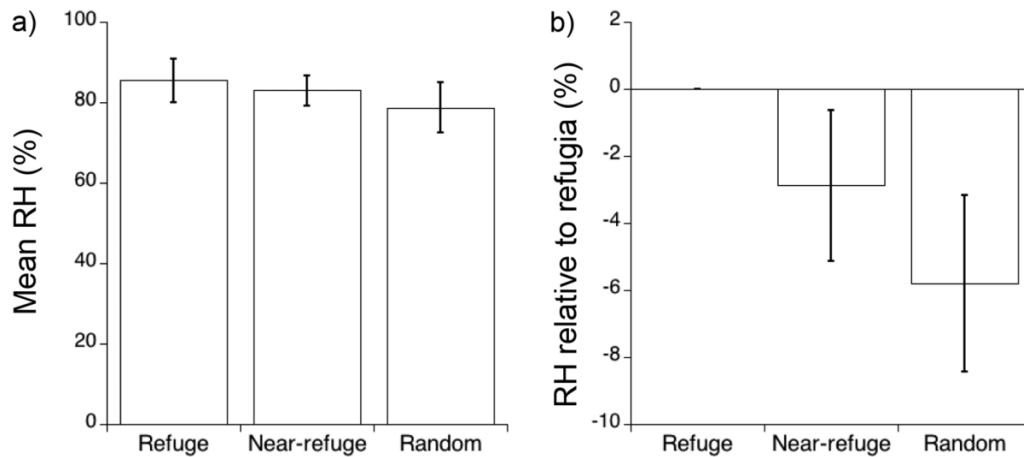
Boreal Toad refugia were different from their surroundings. Toads selected their refugia for favourable microclimates with local-scale increases in RH (Figs. 2a–2b). Several other studies have noted the importance of moist refugia for a variety of anurans, including Crowned Bullfrogs (*Hoplobatrachus occipitalis* (Günther, 1858)) (Spieler and Linsenmair 1998), Wood Frogs (*Lithobates sylvaticus* (LeConte, 1825)) (Baldwin et al. 2006), Natterjack Toads (*Epidalea calamita* (Laurenti, 1768)) (Oromí et al. 2010), and Cane Toads (*Rhinella marina* (L., 1758)) (Seebacher and Alford 2002). Our results prioritized RH over substrate moisture, contrary to the findings of Seebacher and Alford (1999) for Cane Toads. This difference may be the result of interspecific variation, but it might also reflect the relative scales at which moisture measurements were taken; our study measured local-scale (within 20 m) RH variation over relatively short periods ( $22 \pm 3$  days), whereas Seebacher and Alford (1999) used mean monthly trends, presumably describing larger areas.

Our data suggest that Boreal Toads did not select their refugia for specific ground-layer vegetation communities or characteristics. They used a variety of habitat features as refugia (Table 1), and CWD was a substantial component of many. Although there were no differences in CWD among plot categories, CWD did appear to decline with distance from refugia, at least superficially (i.e., rank order). Nevertheless, our initial prediction of CWD being an important structural component of Boreal Toad refugia was not supported.

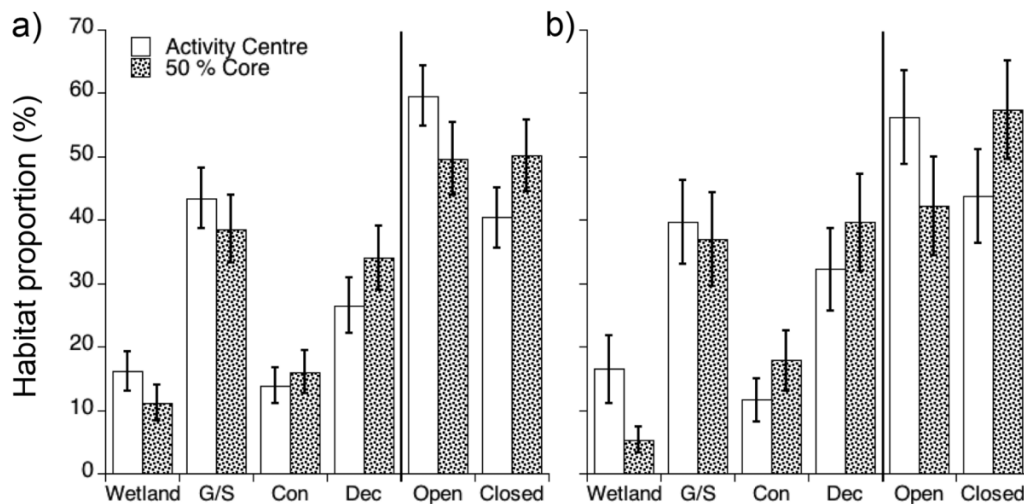
Boreal Toads displayed a number of strategies within the CWD<sub>R</sub> and BRW refuge types. This observation, and the variety of structurally diverse refugia, suggests that Boreal Toads are habitat generalists at fine scales. Other anurans, like the Green and Golden Bell Frog (*Litoria aurea* (Lesson, 1827)) have also been identified as microhabitat generalists (Hamer et al. 2003). The microsites that we examined offered more than simply shelter and relatively moist conditions. Basking sites and the presence of surface water likely represent crucial complementary microhabitats. For instance, Northern Cricket Frogs (*Acris crepitans* Baird, 1854) preferred moist substrates within proximity to shelter and surface water (Smith et al. 2003). These complementary microhabitats may be as important for behavioural thermo- and hydro-regulation as the refugia themselves.

From the six refugia associated with surface water, five were classified as VEG or EXP (Table 1). These refuge types provide abundant escape routes from predators (Spieler and Linsenmair 1998), but the least resistance to desiccation (Seebacher and Alford 2002), despite evidence that shrub-based refugia may provide greater protection from dehydration for Western Toads (Bartelt et al. 2004). The presence of adjacent surface water may be important in offsetting the greater desiccation rates expected for these refuge types.

**Fig. 2.** Relative humidity (RH; mean  $\pm$  SE) by plot category for 10 refugia of Boreal Toads (*Anaxyrus boreas boreas*): (a) raw RH data and (b) RH by categories relative to refugia.



**Fig. 3.** Habitat proportions compared between activity centre and 50% core home-range estimates of Boreal Toads (*Anaxyrus boreas boreas*), presented by stand type and canopy: (a) all (35) individuals and (b) only females (19). G/S, grass and shrub; Con, coniferous; Dec, deciduous.



### Movement behaviour

At the landscape scale, females established refugia farther from breeding sites than males, particularly early in the summer (Fig. 1), supporting the general patterns from several studies of Western Toads (Muths 2003; Bartelt et al. 2004; Bull 2006). Females may quickly disperse following egg deposition to escape male harassment at breeding sites, also giving them the first opportunity to exploit relatively untouched foraging grounds. In contrast, males may tend to remain at breeding sites to increase their chances of encountering late-arriving females and migrate into upland foraging grounds later on.

We were unable to determine a proximate mechanism that could have triggered individuals to abandon established refugia in favour of new habitat. Localized resource depletion and travel distance between patches (both of which increase with patch residence time) were likely influences (Barrette et al. 2010; Townsend-Mehler et al. 2011). Competition for refugia might also have played a role, but we documented a few individuals that displayed a willingness to share refugia with other toads.

The 15 m nocturnal foraging distance represents the local-scale radius to patches of habitat that are actively exploited (i.e., activity centres) where individual knowledge of the landscape would likely be maximal. Individuals most certainly could venture farther than these boundaries in a single night, as suggested by their landscape movement behaviour.

Boreal Toads tended to use linear corridors within a 15 m radius during nocturnal foraging. This suggests that they may not actively seek prey over large areas, but rather consume prey that they encounter while moving, and reposition themselves to ambush prey at alternate locations during the night. The use of downed logs and tunnels as local-scale corridors, as well as the use of suspended or elevated CWD as refugia, also suggests that Boreal Toads make greater use of the three-dimensional habitat structure than previously assumed.

### Habitat use

We were able to illustrate how perception of the landscape can change between fine (local-scale) activity centre and larger home-range estimates, supporting our hypothesis. Our data suggest that open habitat (Fig. 3a), primarily in the

form of wetlands for female toads (Fig. 3b), may be more important at the local scale than previously thought. Boreal Toads are not an obligate forest species and have been reported to prefer open habitat in several other studies (Guscio et al. 2008). When considering landscape disturbance, our data suggest that Boreal Toads should be easy to conserve on the Boreal Plain. This species appears to be a habitat generalist. They occurred within every landscape habitat type in our study and used structurally diverse refugia, exhibited a willingness to cross forest edges as previously described in other studies at a similar latitude (i.e., Deguise and Richardson 2009), and established refugia in clearings (including recent clearcuts). However, nocturnal foraging distances are likely to vary within the global range of Western Toads (e.g., as a function of resource distribution, competition, or climate). Our approach could be valuable for pinpointing critical habitat at the landscape scale, which could be a valuable conservation tool, particularly for populations currently experiencing decline.

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